# Macro-moth families differ in their attraction to light: implications for light-trap monitoring programmes

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**Abstract.** 1. Light traps are used to make inferences about local macro-moth communities, but very little is known about the efficiency with which they attract moths from varying distances, and how this may differ among families.

2. We released 731 marked individuals, from three of the most common and species-rich macro-moth families, at several distances from low-wattage actinic light traps in open and woodland habitat.

3. Logistic regression showed family-specific sampling areas: erebids were attracted from up to 27 m, geometrids from up to 23 m, and noctuids from up to 10 m from the light source, with these distances corresponding to a 5% recapture rate. Sampling size was also family-specific: a maximum of 55% of erebids, 15% of geometrids, and 10% of noctuids were predicted to be trapped when flying near (0–1 m) light traps.

4. Our study demonstrates that weak light traps: (i) have remarkably local sampling ranges, resulting in samples that are highly representative of the local habitat, and (ii) attract small, and family-specific proportions of individuals within these ranges.

5. We suggest that the local sampling ranges of weak light traps make them excellent tools to monitor nocturnal macro-moth communities. As trap efficiency differs among macro-moth families, care must be taken in relating the abundance of the sample to absolute local abundance. Frequent sampling can provide adequate data on relative temporal change in the local macro-moth fauna, however.

**Key words.** Attraction range, biodiversity monitoring, Erebidae, Geometridae, Lepidoptera, mark–release–recapture, moth sampling, Noctuidae, species diversity, standardised sampling.

## Introduction

There is an urgent need to develop a global, co-ordinated system for monitoring biodiversity change to provide scientists and policy makers with representative and timely information on its multi-dimensional aspects (Pereira

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*et al.*, 2013). One way of monitoring change is through population counts for species groups that are easy to monitor and important for ecosystem services (Pereira *et al.*, 2013). Given the numerous ecosystem services provided by the typically highly abundant and ecologically diverse group of macro-moths (e.g. nutrient cycling, pollination: see references in Fox, 2013), and their ease of sampling using light traps (Young, 2005), the establishment of an integrated global monitoring programme to accurately detect and quantify changes in nocturnal macro-moth communities, within a global biodiversity

monitoring framework is highly desirable. Such a programme would be complementary to suggested standardised global sampling programmes for other ecologically important groups, such as butterflies (Basset *et al.*, 2013), dung beetles (Larsen & Forsyth, 2005), and bees (Lebuhn *et al.*, 2013). For example, the latter study has estimated that a global monitoring programme for bees with 200–250 sampling locations would provide sufficient power to detect small annual changes in species richness and total abundance.

Light trapping exploits the tendency of many moth species to approach artificial light sources. They then get trapped through the lobster-pot principle (Waring & Townsend, 2009). There are a number of trap designs, which typically use one of three types of light: standard filament bulbs, mercury vapour (MV) bulbs, and fluorescent actinic tubes (Fry & Waring, 2001). Such automated light trapping is hence a passive sampling method, and it generally outperforms – but not during bright nights at higher latitudes (Pettersson & Franzén, 2008) – other moth sampling methods (such as sugaring and larval surveys), both in terms of numbers of individuals and species caught, and economy of effort (Young, 2005; Waring & Townsend, 2009). Although hand sampling at light may lead to larger samples (Axmacher & Fiedler, 2004; Beck & Linsenmair, 2006), the typically high work load restricts simultaneous sampling at several sites.

Currently, projects that collect standardised macro-moth counts regionally and year-round are ongoing in Britain and Flanders only (Veraghtert, 2012; Fox *et al.*, 2013). The British project revealed that two thirds of common and widespread species have declined over a 40-year period (1968–2007), and across Britain total macro-moth abundance declined by 28%, with a 40% loss in southern Britain (Fox *et al.*, 2013). Similar trends have been shown for The Netherlands, albeit based on non-standardised sampling (Groenendijk & Ellis, 2011). These trends may form part of a wider insect biodiversity crisis (e.g. Conrad *et al.*, 2006; Goulson *et al.*, 2008; Brooks *et al.*, 2012). A global monitoring programme – consisting of a multitude of regional, standardised programmes spread over the world's terrestrial ecosystems – could place these declines within a global context. Despite the relative ease and widespread use of macro-moth sampling with light traps, there are two points that need addressing before rolling out any international macro-moth monitoring programme: (i) To allow comparisons of temporal trends among sites, light traps of identical design should be used, as both lamp type and trap design cause a given bias as to which species, and in what numbers these are sampled (Leinonen *et al.*, 1998; Fry & Waring, 2001; Fayle *et al.*, 2007; Bates *et al.*, 2013). For instance, bigger moth species and noctuids may be attracted more strongly to lamps with smaller wavelengths (van Langevelde *et al.*, 2011; Somers-Yeates *et al.*, 2013). At the same time, a range of abiotic factors, such as temperature, rainfall, wind speed, moonlight, and cloud cover, need to be recorded at trap events to correct for their effects on moth flight activity and trap efficiency (Holyoak *et al.*, 1997; Yela & Holyoak, 1997; Beck *et al.*, 2011). (ii) The gaps in knowledge concerning moths' attraction-to-light behaviour need addressing to understand how the abundance and species composition of the sample relate to the abundance and species composition of the local moth community. With regard to this second point, it is essential to know the proportion of individuals that are attracted to the light trap for a given sampling area surrounding the trap, and how this proportion differs between species and/or families.

Although the effects of light-trap characteristics and environmental factors on the abundance and species composition of moth samples have been well studied (see above), very little is known about the distances at which moths respond to light traps (Ricketts *et al.*, 2001; Hawes *et al.*, 2009; Truxa & Fiedler, 2012). We are aware of only three publications, which all make inferences from the recapture rates (i.e. recapture percentages) of marked moth individuals released at several distances from light traps: (i) the first mark–release–recapture (MRR) experiment on moths by Baker and Sadovy (1978) was conducted on an English lawn for two common and widespread noctuid species, and demonstrated an effective attraction range of about 3 m to MV-light for both species; (ii) Beck and Linsenmair (2006) showed that attraction radii to MV-light differed between sphingids, noctuids, and geometrids within a Southeast-Asian tropical forest, with 50% return rates at distances of *ca.* 10 m for sphingids; and (iii) Truxa and Fiedler (2012) showed that attraction radii to actinic lights are often below 10 m in multi-species experiments within central-European forest habitats. Other studies, using hand sampling at light (15 W actinic), showed marked differences in moth assemblages between undergrowth and canopy at local sites, providing indirect evidence of low attraction radii as species were not drawn towards the different habitats over vertical distances as small as 30–45 m (Beck *et al.*, 2002; Beck & Schulze, 2003).

Here, we examine the effects of a commonly used light trap in macro-moth diversity studies, a Heath-style 6 W actinic trap, on recapture rates of 44 species of macro-moth. Specifically, we test whether: (i) release direction, (ii) release in exposed, open versus sheltered, wooded habitat, and (iii) moth family, contrasting species belonging to the three most common and species-rich macro-moth families, i.e. Erebidae, Geometridae, and Noctuidae, affect individual recapture rates.

We hypothesise the following:

1  that there will be a decreasing recapture rate with increasing release distance from the light trap, and a relatively small overall attraction radius as we used an actinic light source of only 6 W.

2  that recapture rates of individuals released upwind may be higher than for individuals released downwind, as the latter will need to expend more effort to reach the trap.

**3** that recapture rates in an exposed setting will be lower than recapture rates in a sheltered setting, as sheltered flight conditions benefit thermal flight budgets (Merckx *et al.*, 2008), and as background illumination, which decreases trap efficiency (Bowden, 1982), may be higher in an open than in a woodland setting.

**4** that recapture rates may vary considerably with moth family, as light-sensorial and flight-physiological traits may be phylogenetically conserved, resulting in family-specific responses (Beck & Linsenmair, 2006).

## Methods

*Mark–release–recapture*

During eight nights (8–11 and 14–17 June 2010) a total of 731 marked individuals from 44 species belonging to three macro-moth families were released at two sites, one in a woodland and the other in a field habitat (Table 1). The same two sites were used throughout the experiment. The woodland habitat was deciduous woodland within a 22 ha woodland fragment (Bean Wood) situated in

**Table 1.** Numbers of released and recaptured (R) individuals per species, grouped into three macro-moth families, for both field and woodland releases.

| | Field | R Field | Wood | R Wood | Total | R Total |
|---|---|---|---|---|---|---|
| Erebidae | 92 | 3 | 106 | 18 | 198 | 21 |
| *Calliteara pudibunda* | 7 | 0 | 8 | 2 | 15 | 2 |
| *Diaphora mendica* | – | – | 2 | 0 | 2 | 0 |
| *Eilema sororcula* | 26 | 1 | 32 | 4 | 58 | 5 |
| *Herminia grisealis* | 1 | 0 | – | – | 1 | 0 |
| *Hypena proboscidalis* | 1 | 0 | 2 | 0 | 3 | 0 |
| *Laspeyria flexula* | – | – | 1 | 0 | 1 | 0 |
| *Spilosoma lubricipeda* | 23 | 1 | 26 | 5 | 49 | 6 |
| *Spilosoma lutea* | 34 | 1 | 35 | 7 | 69 | 8 |
| Geometridae | 86 | 1 | 89 | 5 | 175 | 6 |
| *Alcis repandata* | 3 | 0 | 5 | 0 | 8 | 0 |
| *Biston betularia* | 2 | 0 | 2 | 1 | 4 | 1 |
| *Campaea margaritaria* | 2 | 0 | 5 | 0 | 7 | 0 |
| *Colostygia pectinataria* | 23 | 1 | 15 | 0 | 38 | 1 |
| *Cyclophora punctaria* | 1 | 0 | 1 | 0 | 2 | 0 |
| *Idaea aversata* | 1 | 0 | – | – | 1 | 0 |
| | 4 | 0 | 3 | 0 | 7 | 0 |

**Table 1.** *(continued)*

| | Field | R Field | Wood | R Wood | Total | R Total |
|---|---|---|---|---|---|---|
| *Lomographa bimaculata* | | | | | | |
| *Lomographa temerata* | 17 | 0 | 14 | 1 | 31 | 1 |
| *Opisthograptis luteolata* | 3 | 0 | 2 | 0 | 5 | 0 |
| *Petrophora chlorosata* | 3 | 0 | 5 | 0 | 8 | 0 |
| *Plagodis dolabraria* | 4 | 0 | 11 | 0 | 15 | 0 |
| *Timandra comae* | 1 | 0 | 5 | 1 | 6 | 1 |
| *Xanthorhoe montanata* | 22 | 0 | 21 | 2 | 43 | 2 |
| Noctuidae | 178 | 0 | 180 | 5 | 358 | 5 |
| *Abrostola tripartita* | – | – | 1 | 0 | 1 | 0 |
| *Agrotis exclamationis* | 39 | 0 | 43 | 2 | 82 | 2 |
| *Agrotis puta* | 1 | 0 | 1 | 0 | 2 | 0 |
| *Anaplectoides prasina* | – | – | 3 | 0 | 3 | 0 |
| *Apamea anceps* | 8 | 0 | 6 | 0 | 14 | 0 |
| *Apamea sordens* | 3 | 0 | 3 | 1 | 6 | 1 |
| *Apamea sublustris* | – | – | 1 | 0 | 1 | 0 |
| *Autographa gamma* | 1 | 0 | 1 | 0 | 2 | 0 |
| *Autographa pulchrina* | 3 | 0 | 1 | 0 | 4 | 0 |
| *Axylia putris* | 4 | 0 | 2 | 0 | 6 | 0 |
| *Charanyca ferruginea* | 1 | 0 | 1 | 0 | 2 | 0 |
| *Charanyca trigrammica* | 30 | 0 | 34 | 1 | 64 | 1 |
| *Craniophora ligustri* | 1 | 0 | 1 | 0 | 2 | 0 |
| *Diachrysia chrysitis* | – | – | 1 | 0 | 1 | 0 |
| *Diarsia mendica* | 24 | 0 | 20 | 0 | 44 | 0 |
| *Diarsia rubi* | 7 | 0 | 9 | 0 | 16 | 0 |
| *Euplexia lucipara* | 1 | 0 | – | – | 1 | 0 |
| *Hoplodrina octogenaria* | 1 | 0 | – | – | 1 | 0 |
| *Mythimna pallens* | 8 | 0 | 10 | 0 | 18 | 0 |
| *Noctua pronuba* | 3 | 0 | – | – | 3 | 0 |
| *Ochropleura plecta* | 15 | 0 | 14 | 1 | 29 | 1 |
| *Xestia c-nigrum* | 27 | 0 | 27 | 0 | 54 | 0 |
| *Xestia triangulum* | 1 | 0 | 1 | 0 | 2 | 0 |
| Grand total | 356 | 4 | 375 | 28 | 731 | 32 |

Wytham Woods, a 400 ha semi-natural forest in southern England (51°46′N, 01°20′W). The field habitat was a large, short-grazed pasture adjacent to the woodland (see Slade *et al.* (2013) for a map and details of the study area). The distance between the two release sites was *ca.* 400 m. All released individuals were caught at light at the edge of Bean Wood (*ca.* 150–300 m from the release sites) the night before release. At dawn, they were individually marked by writing coloured numbers on the hindwing using a permanent, very fine marker (Staedtler Lumocolor), which is a standard and harmless method for MRR experiments on Lepidoptera (Merckx *et al.*, 2009, 2010; Slade *et al.*, 2013). Marked individuals were then placed in mesh insect rearing cages (one for each release distance and habitat), and stored in a cool (*ca.* 15 °C) room until transport to the release sites the same evening.

The releases followed a strict protocol. Every night four releases took place within the woodland and field habitat: two simultaneously a minimum of 1 hour after sunset (i.e. 10.25 pm at the earliest), followed by two more simultaneous releases *ca.* 20 minutes after the first releases (latest release at 11.13 pm). In each one of these release events, marked individuals were simultaneously released at several fixed distances (i.e. 5, 10, 15, 20, 30, 40, 50 m) from a light trap (Heath type, actinic 6 W) positioned at ground level. Individuals were released at four directions (North, East, South, and West) around the light trap (i.e. 28 release points per light trap) (Fig. 1). The woodland trap location was away from paths or rides, which may facilitate moth flight (Mönkkönen & Mutanen, 2003), and may hence bias recapture rates (Beck & Linsenmair, 2006; Truxa & Fiedler, 2012). We spread the individuals available each night across the range of release distances and between the habitats to evenly cover both woodland and open habitat during the experiment (Tables 1 and 2). Exactly 10 minutes after each simultaneous release, we recorded all marked individuals that were found sitting on or inside the light trap. This 10-minute interval was considered sufficient to allow moths to reach take-off body temperature, and then to fly up to 50 m towards the light trap. This consideration was based on preliminary tests involving a set of both early- and late-night species from the three families. Overall nocturnal moth activity in Europe is generally known to be highest during the first hour after nightfall (i.e. our experimental time window), although inter-specific variation in activity does exist, with some species only flying later at night. Based on the preliminary tests, we found that even late-flying species are stimulated to take-off as soon as possible upon release, probably aiming to escape the handling disturbance. We did not test all the species, however, and it is possible that some individuals may have remained inactive upon release. Recaptures of moths that were released from an earlier session were excluded from the analyses (two individuals after 20 minutes, one after 28 minutes) as we could not exclude the possibility that these individuals took-off in a direction away from the light trap and then later returned to within the attraction radius.

Data loggers were placed at a height of 1 m at each of the release sites, recording ambient temperature every 10 minutes. Temperatures recorded during the experiment (22 h 20–23 h 20) at the field release site were on average 1.3 °C lower than those recorded at the woodland site (mean ± SE (°C): 11.3 ± 0.40 vs. 12.6 ± 0.37, respectively). All releases took place under light breezy (6–12 km h$^{-1}$), new moon (12th June), and dry conditions.

### Analyses

Given that all releases took place under similarly favourable conditions, data from all release sessions were combined for each habitat. We then tested for an overall effect of release direction on recapture rates with the Pearson's $\chi^2$-test. As there was no difference in the relative number of recaptures originating from the four release directions, release directions were combined within subsequent analyses. As such, sample sizes at each of the seven release distances were large enough to allow for meaningful analyses and conclusions (Table 2). We then tested for an overall effect of release habitat using the Pearson's $\chi^2$-test with Yates' continuity correction to prevent overestimation of statistical significance.

As we observed both a much higher overall recapture rate at the woodland habitat than at the field habitat (Fig. 2) and too few recaptures at the field habitat for meaningful analyses, all subsequent analyses were then done for the woodland releases only. Given the binary nature of the response variable (i.e. recaptured or not), generalised linear models with a 'logit' link function were run to model the relationship between the attraction-to-light behaviour and the following explanatory
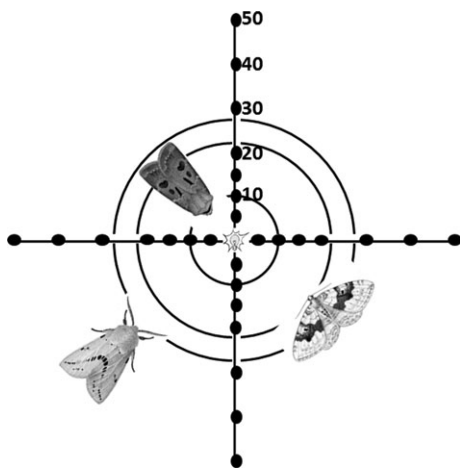


**Fig. 1.** Release set-up: dots depict the 28 release points around each light trap at distances of 5, 10, 15, 20, 30, 40, and 50 m. Circles indicate attraction radii for three macro-moth families, at which a minimum of 5% of individuals present are recaptured. Outer circle: Erebidae; middle circle: Geometridae; inner circle: Noctuidae (within woodland; see also Fig. 3).

**Table 2.** Numbers of released and recaptured (R) macro-moth individuals at each release distance, per family, for both field and woodland releases.

|  | Field | RField | Wood | RWood |
|---|---|---|---|---|
| Erebidae | 92 | 3 | 106 | 18 |
| 5 | 16 | 2 | 17 | 7 |
| 10 | 15 | 1 | 16 | 6 |
| 15 | 14 | 0 | 17 | 3 |
| 20 | 12 | 0 | 16 | 1 |
| 30 | 6 | 0 | 12 | 1 |
| 40 | 15 | 0 | 13 | 0 |
| 50 | 14 | 0 | 15 | 0 |
| Geometridae | 86 | 1 | 89 | 5 |
| 5 | 17 | 1 | 19 | 3 |
| 10 | 10 | 0 | 13 | 1 |
| 15 | 8 | 0 | 6 | 0 |
| 20 | 9 | 0 | 9 | 0 |
| 30 | 12 | 0 | 9 | 0 |
| 40 | 15 | 0 | 14 | 0 |
| 50 | 15 | 0 | 19 | 1 |
| Noctuidae | 178 | 0 | 180 | 5 |
| 5 | 30 | 0 | 25 | 2 |
| 10 | 26 | 0 | 25 | 1 |
| 15 | 21 | 0 | 22 | 1 |
| 20 | 31 | 0 | 28 | 0 |
| 30 | 22 | 0 | 25 | 1 |
| 40 | 17 | 0 | 20 | 0 |
| 50 | 31 | 0 | 35 | 0 |
| Grand total | 356 | 4 | 375 | 28 |

variables: release distance (continuous), macro-moth family (categorical: three classes), and their interaction. These logistic regression models did not display overdispersion or any pattern in the residuals versus the fitted values, and the normal plots were close to linear. The distance variable was not log transformed as doing so increased residual deviance. Z-tests were run to test for differences in recapture rate among families. As the distance × family interaction turned out to be non-significant, the interaction was removed from the final model. Coefficients from the final model were used to predict mean sampling distances for given recapture percentages. R was used for all analyses (R Development Core Team, 2011).

## Results

Overall, there was no difference in the relative number of recaptures originating from the four release directions ($\chi^2_3 = 2.84$, $P = 0.42$), but there was a much higher overall recapture rate at the woodland habitat than at the field habitat (7.5% vs. 1.1%, respectively; $\chi^2_1 = 19.07$, $P < 0.0001$) (Fig. 2). Only four individuals from a total of 356 released individuals were recaptured at the field habitat, whereas the woodland releases resulted in a total of 28 recaptures from 375 released individuals (Tables 1 and 2).

Based on the woodland release data, the logistic regression showed a strong overall effect of a decreasing recapture rate with increasing distance from the light source ($z = -3.73$, $P = 0.002$) (Figs 2 and 3). Although this distance effect was present for all three macro-moth families (family × distance: $F_{2, 19} = 1.13$, $P = 0.32$), erebids showed higher overall recapture rates than geometrids ($z = -2.40$, $P = 0.017$) and noctuids ($z = -3.68$, $P = 0.0002$), which were especially marked at relatively short distances from the light source (i.e. <20 m) (Figs 2 and 3). We found family-specific responses in recapture rates and attraction radii: erebids were attracted from up to $27 \pm 5$ m, geometrids from up to $23 \pm 12$ m, and noctuids from up to $10 \pm 6$ m from the light source, with these specific distances corresponding to a 5% recapture rate (Fig. 1). Sampling size was also family specific: a maximum of 55% of erebids, 15% of geometrids, and 10% of noctuids were predicted to be attracted when flying near (0–1 m) light traps (Fig. 3).
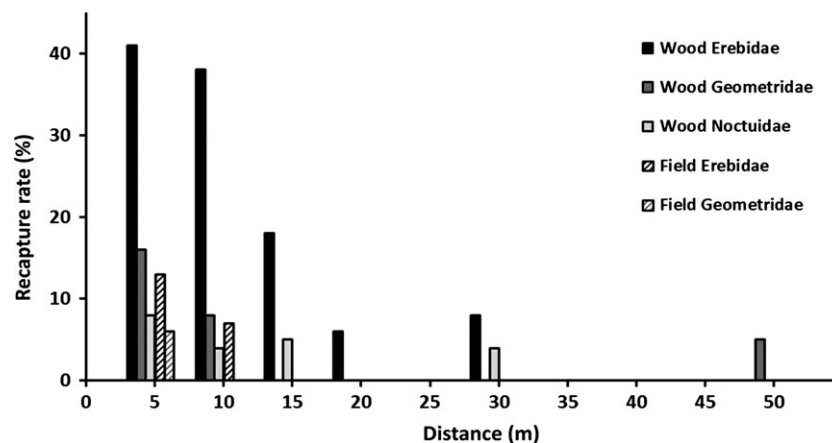


**Fig. 2.** Observed percentage of recaptured macro-moth individuals as a function of release distance (m), in field and woodland habitat, and for three macro-moth families. Note that no individuals were released at distances of 25, 35, 45, and 55 m.
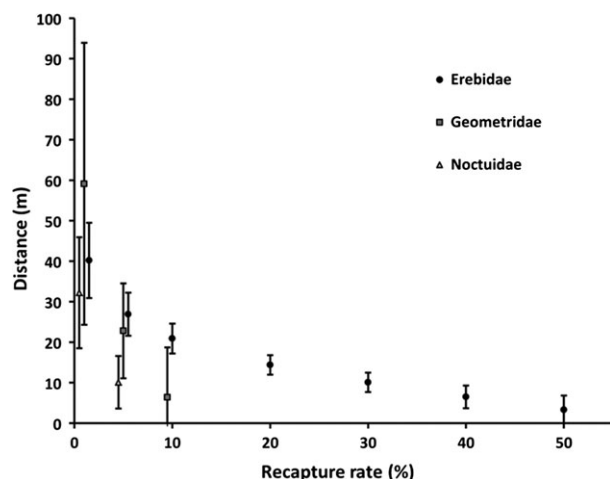
**Fig. 3.** Modelled sampling distance (m ± SE) from the light source as a function of recapture percentages, in woodland habitat, for three major macro-moth families. Data points at 1, 5, and 10% are slightly jittered to improve clarity.

Although the number of recaptures is relatively small, the actual sample size (i.e. number of releases) used for the logistic regression is relatively large. As such, we believe that the demonstrated family-specific effects are robust, especially as these effects do not appear to be driven by one or two dominant species, but result from the combined responses of a fairly large number of species for each of the three families (Table 1). Nevertheless, it would be good to test whether our family-specific differences hold when testing a different set of species.

## Discussion

*Attraction to light: light intensity*

We show that the recapture rate of macro-moths decreases with increasing release distance from the light trap (see also Baker & Sadovy, 1978; Beck & Linsenmair, 2006; Truxa & Fiedler, 2012), and this was true for all three families tested. In contrast to the relatively bright lights used in previous attraction-to-light studies, we are the first to publish results of the common 6 W Heath-type light traps. Advantages over other wattages and light types are that they can emit light over long time periods from a light-weight 12 V battery, and that they are relatively cheap, inconspicuous, and portable. As expected, we obtained lower overall attraction, and smaller attraction radii, than studies which used stronger lights. For example, Beck and Linsenmair (2006) found that >10% of Southeast-Asian tropical forest sphingids released 105–120 m from a 125 W MV-light were recaptured within 5 minutes. Truxa and Fiedler (2012) tested 2 × 15 W actinic tubes and reported intermediate recapture characteristics for Central-European forest moths. For example, 7% of geometrids were recaptured within 5 minutes when

released up to 80 m away. Contrastingly, in our study the largest recapture distance for erebids and noctuids was 30 m, with the majority within 10 m, and with relatively low overall recapture rates. For example, the modelled recapture percentage of moths released at 3 m was only 5–10% for noctuids, 10–15% for geometrids, and 50% for erebids, whereas Truxa and Fiedler (2012) reported recapture rates of 19–39% at 3 m. These percentages are higher than our geometrid and noctuid percentages, in line with the stronger light. Yet, they are lower than our erebid percentage, but as Truxa and Fiedler (2012) combined noctuids and erebids into one super-family, individual family effects may have been obscured.

*Attraction radii: 50% vs. 5% approach*

Attraction radii have been defined as distances at which 50% of released individuals are predicted to be recaptured within 5 minutes (Beck & Linsenmair, 2006). Given that this approach: (i) often leads to negative values, which are difficult conceptually, and (ii) does not inform on the larger distances from which a smaller proportion of individuals are still drawn in, we suggest redefining attraction radii as distances from light sources at which 5% of individuals present are still attracted to these lights. For example, using the 50% approach, Beck and Linsenmair (2006) report a negative attraction radius for geometrids, a 13 m radius for noctuids, and a 10 m radius for sphingids, with radii for individual sphingid species between negative values and 26 m. This 50% approach hence risks concluding, wrongly, that geometrids are drawn in from shorter distances than sphingids and noctuids. The 5% approach leads to conclusions which better fit the observed attraction-to-light behaviour, with noctuids having the smallest, geometrids intermediate, and sphingids the largest attraction radii (>120 m). We therefore believe that the 5% approach improves interpretability when comparing light-trap characteristics regarding moths' attraction-to-light behaviour.

*Environmental factors*

Although we cannot generalise, we are the first to show that recapture rates in a high-visibility field are lower than in woodland. We believe that the almost seven times difference in recapture rates results from two complementary factors: thermoregulation and background illumination. Ambient temperature was on average 1.3 °C lower for field releases, which may have increased individual warm-up times to reach thoracic flight take-off temperatures (Heinrich, 1974), especially given the extra chill factor due to the exposed conditions (Merckx *et al.*, 2008). The openness also meant that skyglow was visible (Oxford city centre was 5 km from the release sites), which is known to decrease light-trap efficiency (Bowden, 1982). We call for experimental research to disentangle the relative

impact of the effects of: (i) lower trap efficiency due to light pollution, (ii) lower moth abundance due to light pollution, and (iii) lower moth abundance due to thermo-regulatory constraints, all three of which likely interact at open sites within human-dominated landscapes characterised by light-polluted night skies.

Under light breezy conditions there was no difference in the relative amount of recaptures originating from the four release directions, suggesting that wind direction has no effect on recapture rates under light breezy conditions.

### Family-specific responses

In line with our hypothesis, we found clear family-specific responses in recapture rates and attraction radii, with erebids and geometrids attracted from further away than noctuids. As such, we show that the sampling area around light traps differs among three main macro-moth families. Moreover, relative to the number of erebids recaptured, geometrids are approximately four, and noctuids more than five times less likely to be recaptured. Such differences are probably due to differences in light-sensorial and flight-physiological (e.g. flight velocity) traits, which may be phylogenetically conserved (Beck & Linsenmair, 2006). For instance, distances from which these families are drawn to light could correlate with their general mobility. Based on MRR data collected within the same landscape, model-predicted distances moved (m ± SE) suggested that noctuid species (287 ± 38 m, $N = 38$) are generally more mobile than geometrid and erebid species (170 ± 20 m, $N = 22$; 173 ± 28 m, $N = 11$, respectively) (Slade *et al.*, 2013). Here, we show that mobile noctuids are attracted to light from closer than less mobile erebids and geometrids. Beck and Linsenmair (2006) also showed family effects for tropical macro-moths, but with typically mobile sphingids attracted from furthest away. Nevertheless, we remark that any phylogeny-based behavioural inference is inherently a generalisation, and that the morphological and flight-behavioural inter-specific diversity within entire macro-moth families may be substantial.

### Representativeness of light-trap samples

Our study confirms that light traps have remarkably local sampling ranges, which results in samples highly representative of local conditions, hence contradicting the popular belief that light traps draw in moths from distances of up to 500 m (Bowden & Morris, 1975; Baker & Sadovy, 1978; Bowden, 1982). The increasing need to relate moth samples from light traps with surrounding habitat and landscape characteristics requires better knowledge of the spatial resolution of light traps (Hawes *et al.*, 2009; Fuentes-Montemayor *et al.*, 2011, 2012; Merckx *et al.*, 2012a,b). MRR studies, using light traps positioned across landscapes, are increasingly being used to study macro-moth movements and dispersal (Nieminen,

1996; Merckx *et al.*, 2009, 2010; Slade *et al.*, 2013). The key assumption of these studies is that macro-moths move naturally and are not being drawn towards traps over large distances. Our results show that low-wattage traps fulfil this assumption.

For moth monitoring programmes, where maximising catches is not the aim, low capture rates and short attraction distances are positive aspects of using less powerful light sources (Leinonen *et al.*, 1998). Relatively small samples speed up identification/processing, and short attraction distances guarantee that samples are representative of the local environment.

### Implications for a global light-trap monitoring programme

The local sampling ranges and low capture rates of low-wattage light traps make them excellent tools to monitor macro-moth communities in well-defined habitats (see also Truxa & Fiedler, 2012). By implementing one trap design at single locations, frequent sampling can provide a sound tool to assess temporal changes in the macro-moth fauna, even if macro-moth species and families are attracted to different degrees. The inclusion of such local sampling within regional networks, using a similar methodology, allows the assessment of relative temporal changes among habitats and regions. Our finding that recapture rates were much lower in an open versus a closed habitat may, however, imply that observed temporal change at sites with changing degrees of openness (e.g. forest–savannah dynamics) is due to a combination of real change and sampling bias. Given their significant ecological roles, we conclude by recommending the establishment of a standardised light-trap monitoring programme to detect detailed population change for macro-moth species within a global framework.

### Acknowledgements

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